

Fig. 3. Plot of first two axes from a principal component analysis of 21 morphometric characters of mixed sexes of *Oreochromis niloticus* strains: E = Egypt; G = Singapore; H = Ghana; I = Israel; K = Kenya; S = Sénégal; T = Thailand; W = Taiwan.

the Philippines designed to do linear measurements of objects on a photographic image. The program gives

good accuracy for each measurement session since it verifies the plane of projection of the image. The data are filed as Lotus 123 worksheets and are log-transformed to reduce homoscedasticity of variances. To correct for size effects, each observed distance is divided by its estimate. Corrected size measurements were analyzed multivariately under the Principal Component Analysis and was performed using the Statistical Analysis System (SAS) software.

A typical result (Fig. 3) shows the separation of Kenya strain *O. niloticus* from a cluster of 'Philippine' and African strains. This indicates that overall shape of Kenya strain is different from the rest of the strains, being shorter and having a streamlined body (Eknath et al. 1991). The

overlapping pattern of separation among the strains (except Kenya) indicate that these strains are weakly differentiated. The greater segregation of the Kenya strain from others supports its subspecific status: *O. niloticus vulcani*, the other strain being *O. n. niloticus* (Trewavas 1983).

References

- Brzeski, V.K. and R.W. Doyle. 1988. A morphometric criterion for sex discrimination in tilapia, p. 439-444. In R.S.V. Pullin, K. Bhukaswan, K. Tonguthai and J.L. Maclean (eds.) The Second International Symposium on Tilapia in Aquaculture. ICLARM Conf. Proc. 15, 623 p.
- Eknath, A.E., J.M. Macaranas, L.Q. Agustin, R.R. Velasco, M.C.A. Ablan, M.J.R. Pante and R.S.V. Pullin. 1991. Biochemical and morphometric approaches to characterize farmed tilapias. Naga, ICLARM Q. 14(2):7-9.
- Libosvasky, J. and N.F. Bishara. 1986. Variability of morphometric characters in four Egyptian tilapiine fishes. Folia Zoologica 36(3):265-272.
- Trewavas, E. 1983. Tilapiine fishes of the genera *Sarotherodon*, *Oreochromis* and *Danikilia*. British Museum (Natural History), London, 583 p.

Growth Performance in Fishes: Rigorous Description of Patterns as a Basis for Understanding Causal Mechanisms*

Abstract

The origins and features of the growth performance index ϕ' are reviewed, emphasizing its ability to express the underlying common characteristics of a family of growth curves. Some other aspects of ϕ' are discussed, notably its correlation, in fishes, with functional morphology (e.g., gill surface area for respiration) and its conceptual links with *auximetric grids*, another device proposed by the author for growth comparisons of fishes.

Introduction

The Random House Dictionary defines *comparison* as "the considering

DANIEL PAULY

ICLARM

MC P.O. Box 1501

Makati, Metro Manila, Philippines

of two things with regard to some characteristic that is common to both, as the likening of a hero to a lion in courage". The growth curves of fishes even of the same species and population can be very different, and comparing them is indeed difficult. This is because growth relates *two* variables, (i) size and (ii) time.

Therefore, when two growth curves e.g., are to be compared, at least *four* numbers are implied, which when left

unconsidered, can quickly lead to contradictions. For example, Kinne (1960) wrote, upon comparing the growth curves of guppies:

"The results indicate that the differences in growth rate established in young fish do not persist throughout life. Initially slow-growing fishes may surpass initially fast-growing fishes, and finally reach a greater length-at-age."

Pauly (1979) attempted to deal with this and similar problems. One of the key results was that, given von Bertalanffy growth curves, when one plots, for many different fish species, population-specific values of $\log K$ against their corresponding values of

*ICLARM Contribution No. 793.

$\log L_{\infty}$, the mean slope one obtains is 2. Hence, in general

$$\log_{10} K = a + 2 \log L_{\infty} \quad (1)$$

with "a" being a species-specific constant, for which the theory of von Bertalanffy (1938, 1951) provides ample theoretical reasons, not discussed here.

The potential uses of this relationship were described by Pauly (1980a, 1980b), but received little attention until reappraisal of work on Caribbean coral reef fishes (Munro 1983) required an index for comparing their growth. Munro and Pauly (1983) then presented

$$\log_{10} K = \phi' + 2/3 \log W_{\infty} \quad (2)$$

This was followed by Pauly and Munro (1984), where equation (1) was restyled (with "a" renamed ϕ') and where a rather embarrassing error in the original text of Munro and Pauly (1983) was corrected.

The ϕ' index (i.e., equation 1) has been widely used, mainly because it was taught during successive FAO/DANIDA training courses in Tropical Fish Stock Assessment (see contributions in Venema et al. 1988). The index became also known to aquaculturists because Jacques Moreau (of the Ecole Nationale Supérieure Agronomique de Toulouse, France) and I cooperated on a series of papers on ϕ' applied to tilapias (Moreau et al. 1986; Pauly et al. 1988a, 1988b) and because others began to write about it in ICLARM publications (Vakily 1988; Mathews and Samuel 1990).

This wide use of the ϕ' index inevitably implied that misunderstandings as to its applicability would come up, and Dr. Kevin Hopkins' letter to the Editor of *Aquabyte* (see Addendum, p. 6) illustrates this. Obviously, his three growth curves for pond A2, B2 and C2 (Fig. A1) are "different" (i.e., suggesting different growth rates for every age or size) just like the hero and the lion in the above definition of 'comparison' are. But *what* is it that they have in common?

What they have in common is precisely that two times the log of their asymptotic size (L_{∞}), plus the log of

their curvature parameter (K) leads to a constant ($\phi' = 3.40$), which itself defines a family of growth curves (Fig. 1B).

As might be seen, this family of growth curves differs from that defined, e.g., by $\phi' = 3.00$ (Fig. 1A) or $\phi' = 3.80$ (Fig. 1C).

Another way of expressing this is using another concept proposed for comparing growth performance, the *auximetric grid* (Pauly 1979): essentially a plot of $\log K$ vs $\log L_{\infty}$ (or W_{∞} , not considered here). On such plots, families of growth curves such as on Fig. 1 are expressed by points on lines of slope 2 and intercept ϕ' , with each point representing a growth curve (Fig. 2). What Fig. 2A implies, thus, is that fishes of a certain genotype will either have a low K and a high L_{∞} or *vice versa*, but will stay on the same line (i.e., have the same ϕ').

Generally, it is *stress* (Selye 1980) which makes L_{∞} decrease, and K increases, which is why I refer to von Bertalanffy's K as a *stress factor* in Pauly (1979). Examples of stresses are high temperature, low density of food, being low in some pecking order, diseases, etc.

What these various forms of stress have in common, is that they cause elevated metabolism; O_2 consumption, however, cannot be increased at will, as it is ultimately limited by available gill surface area. Thus, one finds, as expected, that ϕ' is a strong correlate of gill surface area (Pauly 1979; Longhurst and Pauly 1987; Fig. 3). [This stress also is what induces maturation, and this is the reason why there is, in fish, a strong correlation between mean size at first maturity (L_m) and asymptotic size (L_{∞}), with L_m/L_{∞} constant within a species (Pauly 1984)].

I am aware that things are more complicated than that, and that not all fish - not even siblings - react similarly

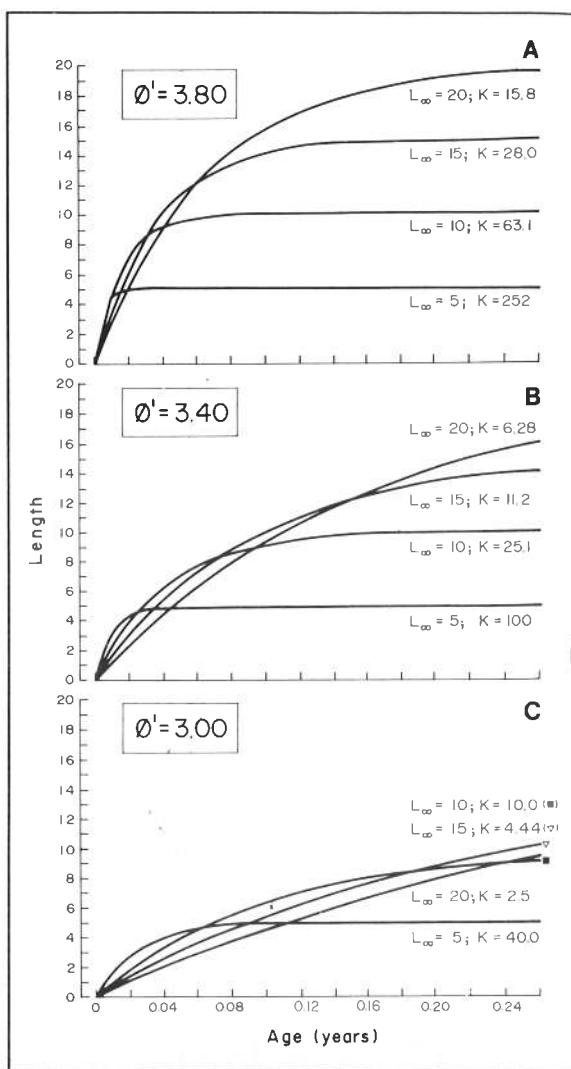


Fig. 1. Three families of growth curves, each with the same value of $\phi' = \log_{10} K + 2 \log L_{\infty}$, and all assuming that $t_0 = 0$.

- A: $\phi' = 3.80$, for values of $L_{\infty} = 20, 15, 10$ and 5.
- B: $\phi' = 3.40$ (as in K. Hopkins' communication, see Addendum, p. 6), for the same values of L_{∞} as in A.
- C: $\phi' = 3.00$, for L_{∞} values as in A and B.

Note that some of the extreme parameter combinations will not occur in reality; these examples (all drawn at the same scale of length and age) nevertheless document how different values of ϕ' define different families of curves.

to a given stress. This is the reason why growth curves of fish do not, in reality, align themselves as neatly as suggested in Fig. 2A, but rather form clusters of points, such as illustrated in Fig. 2B.

These clusters can be analyzed and compared, too, and a first attempt at this, and an appropriate software called AUXIM, are presented by Pauly et al. (in press) (see also Fig. 2C).

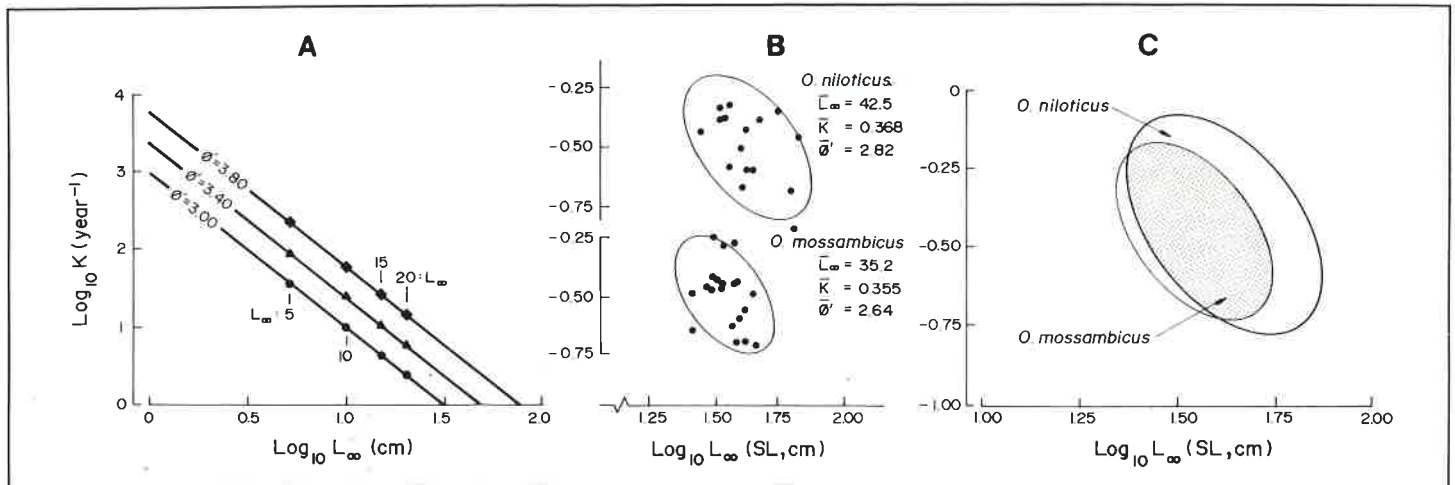


Fig. 2. Auximetric grids for comparison of growth performance in fishes (adapted from Pauly et al., in press).

- A: Shows how the curves in the three panels of Fig. 1 can be represented as points on three lines each defined by its ϕ' .
- B: Shows the scatter of points representing typical growth curves of Nile and Mozambique tilapia (*Oreochromis niloticus* and *O. mossambicus*), and expressing the variance around estimates of ϕ' ; SL = standard length.
- C: Shows an area-based approach for growth comparison and an overlap index quantifying their (niche?) overlap (here: 0.553, for an index ranging from 0 to 1); SL = standard length.

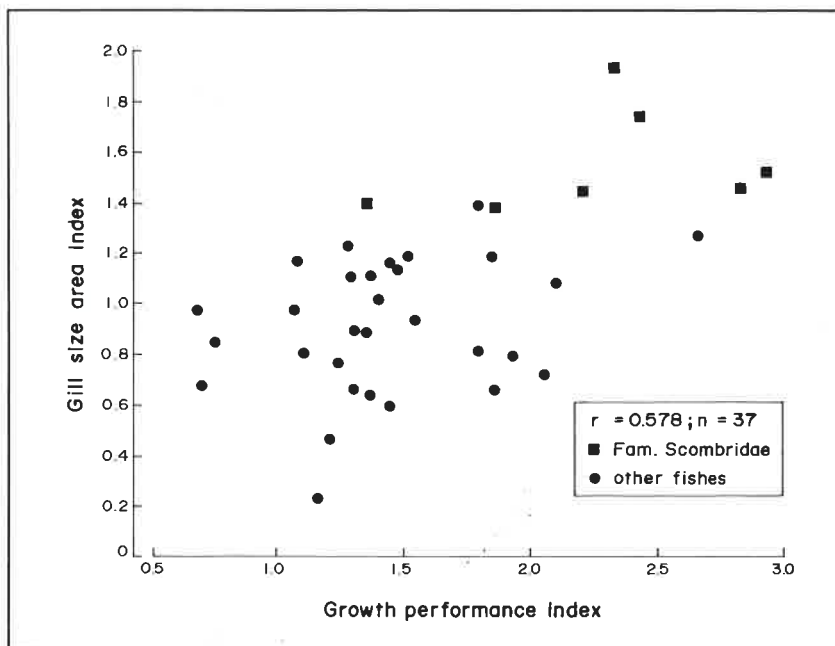


Fig. 3. Correlation in fishes between the growth performance index ϕ' (see equation 2) and an index of gill size area (= log of a, where a is taken from a relationship of the form: gill area = $a \cdot W^d$, where W is body weight and d is an exponent ranging from 0.6 to 0.9) (adapted from Pauly 1979, 1985).

Conclusion

The growth performance index ϕ' does not define any specific growth curve, and hence, if this is what one is interested in, ϕ' is rather useless, and even misleading. On the other hand, ϕ' expresses a commonality between the growth patterns of different fishes. This

is useful for stock assessment, to estimate K from L_{∞} , and also may be useful for evaluation of growth performance potentials under a variety of environmental stresses, e.g., under aquaculture conditions (Pauly 1987; Mathews and Samuel 1990). Let's hope there will be no more misunderstandings.

Acknowledgement

I thank Kevin Hopkins for stimulating me to write this.

References

- Kinne, O. 1960. Growth, food intake, and food conversion in an euryplastic fish exposed to different temperatures and salinities. *Physiol. Zool.* 33:288-317.
- Longhurst, A.R. and D. Pauly. 1987. *Ecology of tropical oceans*. Academic Press, San Diego, California. 407 p.
- Mathews, C.P. and M. Samuel. 1990. Using the growth performance index ϕ' to choose species for aquaculture: an example from Kuwait. *Aquabyte* 3(2):2-4.
- Moreau, J., C. Bambino and D. Pauly. 1986. A comparison of four indices of overall growth performance, based on 100 tilapia populations (Fam. Cichlidae), p. 201-206. In J.L. Maclean, L.B. Dizon and L.V. Hosillos (eds.) *The First Asian Fisheries Forum*. Asian Fisheries Society, Manila, Philippines.
- Munro, J.L., Editor. 1983. *Caribbean coral reef fishery resources*. ICLARM Stud. Rev. 7, 276 p.
- Munro, J.L. and D. Pauly. 1983. A simple method for comparing the growth of fish and invertebrates. *Fishbyte* 1(1):5-6.
- Pauly, D. 1979. Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula. *Ber. Inst. f. Meeresk. Univ. Kiel*, No. 63, XV + 156 p.
- Pauly, D. 1980a. A selection of simple methods for the assessment of tropical fish stocks. *FAO Fish. Circ.* No. 729, 54 p.
- Pauly, D. 1980b. A new methodology for rapidly acquiring basic information on tropical

fish stocks: growth, mortality and stock-recruitment relationships, p. 154-172. In S. Saila and P. Roedel (eds.) Stock assessment for tropical small-scale fisheries. University of Rhode Island, International Center for Marine Resources Development, Kingston, Rhode Island.

Pauly, D. 1984. A mechanism for the juvenile-to-adult transition in fishes. *J. CIEM* 41:280-284.

Pauly, D. 1985. Zur Fischereibiologie tropischer Nutztiere: eine Bestandsaufnahme von Konzepten und Methoden. (Habilitationsschrift). Ber. Inst. Meeresk. Univ. Kiel No. 147, 155 p.

Pauly, D. 1987. Application of information on age and growth to fishery management, p. 495-506. In R.C. Summerfeldt and G.E. Hall (eds.) The age and growth of fish. The Iowa University Press, Ames.

Pauly, D. and J.L. Munro. 1984. Once more on growth comparison of fish and invertebrates. *Fishbyte* 2(1):21.

Pauly, D., J. Moreau and M.L. Palomares. 1988a. Detritus and energy consumption and conversion efficiency of *Sarotherodon melanotheron* (Cichlidae) in a West African lagoon. *J. Appl. Ichthyol.* 4:150-153.

Pauly, D., J. Moreau and M. Prein. 1988b. Comparison of growth performance of tilapia in open waters and aquaculture, p. 469-479. In R.S.V. Pullin, T. Bhukasawan, K. Tonguthai and J.L. Maclean (eds.) The Second International Symposium on Tilapia in Aquaculture. ICLARM Conf. Proc. 15, 623 p.

Pauly, D., J. Moreau and F. Gayanilo, Jr. 1991. A new method for comparing the growth performance of fishes, applied to wild and farmed tilapias. Paper presented at the Third International Conference on Tilapia in Aquaculture, Abidjan, Côte d'Ivoire, 11-16 November 1991. (In press).

Selye, H. 1980. The stress concept today, p. 127-143. In E.L. Kutash, L.B. Schlesinger and Associates (eds.) Handbook of stress and anxiety: contemporary knowledge, theory and treatment. Jossly-Bass Inc., San Francisco.

Vakily, J.M. 1988. Estimation and comparison of fish growth parameters from pond experiments: a spreadsheet solution. ICLARM Software 3, 12 p.

Venema, S., J. Möller-Christensen and D. Pauly, Editors. 1988. Contributions to tropical fisheries biology: papers by the participants of FAO/DANIDA follow-up training courses. FAO Fish. Rep. No. 389, 519 p.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (Inquiries in growth laws II) *Hum. Biol.* 10(2):181-213.

von Bertalanffy, L. 1951. Theoretische Biologie - Zweiter Band: Stoffwechsel, Wachstum. A. Francke A.G. Verlag, Bern, 418 p.

Addendum

Dr. Kevin Hopkins of the University of Hawaii at Hilo (College of Agriculture, Hilo, Hawaii 96720, USA) has communicated the following opinion on the use of ϕ' . References cited in this communication can be found in the preceding reference list. - Editor

ϕ' is not Suited to Compare Growth in Pond Experiments

Moreau et al. (1986) proposed a single parameter, ϕ' , for use in comparing growth performance of fish. This parameter is computed from the K and L_{∞} of the von Bertalanffy Growth Function and was used by Moreau et al. (1986) to compare 100 tilapia populations. Another 150 tilapia "stocks" were compared using ϕ' by Pauly et al. (1988b). The computation

of ϕ' is a feature in the computer program to estimate fish growth parameters by Vakily (1988).

As part of my work with tilapia growth in pond fertilization experiments, ϕ' has been routinely calculated using the program of Vakily. Examination of the results of those calculations casts considerable doubt on the efficacy of using ϕ' to compare treatments in pond experiments. Fig. A1 shows the average length at time of tilapia in three different ponds during a recent experiment at the Asian Institute of Technology (AIT) in Thailand. Although ϕ' is identical (3.40) in all three ponds, it is readily apparent that the growth responses were very different.

I suggest that the statement used by Moreau et al. to start their 1986 paper also applies to ϕ' :

"Growth comparisons of fish based on a single parameter have been found to be misleading."

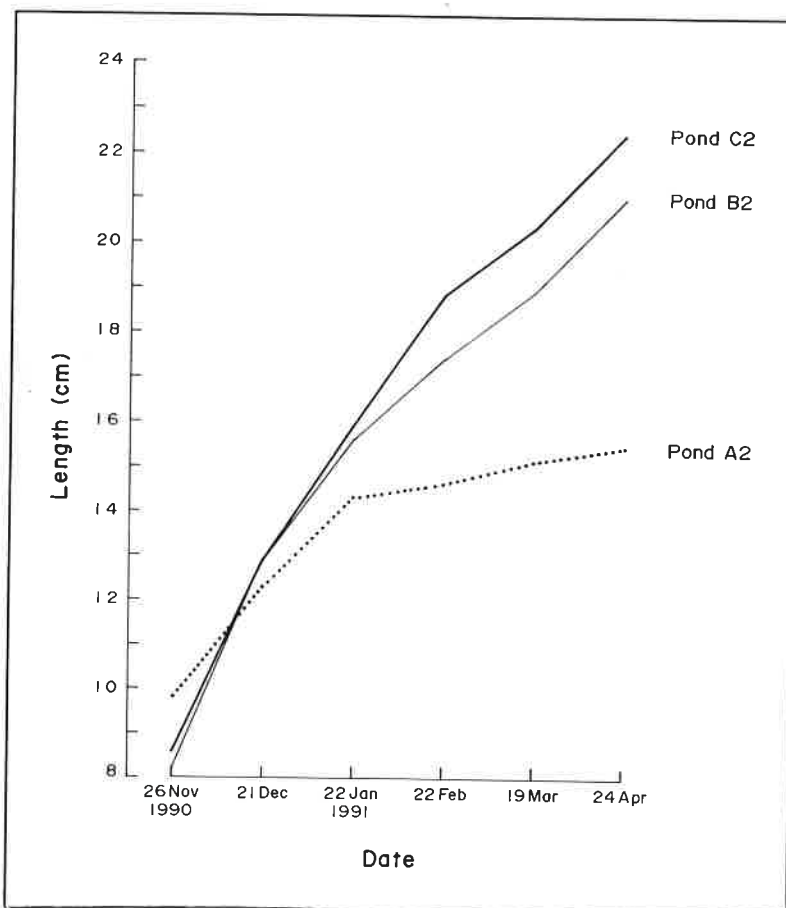


Fig. A1 Average growth (in cm, total length) of *Oreochromis niloticus* in three ponds during an experiment at the Asian Institute of Technology, Thailand (all three curves lead to $\phi'=3.40$).